Competitive N uptake between rice and weedy rice

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Abstract

Weedy rice, red rice (*Oryza sativa* L.), is a serious problem in rice-producing areas of the southern U.S. and various regions worldwide. It competes for production inputs, increases weed control cost, reduces yield and grain quality, and could eliminate economic returns. Research was conducted to compare: (i) the relative efficiencies of rice and weedy rice in recovering fertilizer N under a competitive condition, (ii) the accumulation and partitioning of N by rice and weedy rice, and (iii) the N use efficiency of rice and weedy rice. Experiments were conducted in 1999 and 2000 at the Rice Research and Extension Center, Stuttgart, Arkansas, USA. Experimental units were arranged in a split–split plot design with N rate (0, 5, 10, 15, and 20 g m^{-2}) as mainplot, plant type (rice and weedy rice) as subplot, and type of shoot tissue (lower leaf, leaf sheath, top leaf, and panicle) as the sub-subplot. 'Drew' rice and strawhull weedy rice were drill-seeded in alternate rows. At 26–27 days after planting, metal collars were driven into the soil to establish two microplots per treatment. Urea labeled with ^{15}N was applied to dry soil in the microplots immediately before permanent flood. Data were collected at panicle initiation (PI) and 2 weeks after heading (WAH). Regardless of growth stage, Drew rice and weedy rice produced equivalent shoot biomass when no fertilizer N was added. At PI, both plant types showed a quadratic response to fertilizer N with respect to biomass production. However, where the response to N was positive, weedy rice accumulated 42 g shoot biomass g^{-1} of added N whereas shoot biomass accumulation for Drew was 33 g g^{-1} of added N. Overall, weedy rice accumulated more biomass than rice upon addition of N fertilizer. The difference in shoot biomass production between Drew and weedy rice became larger as the growing season progressed. At 2 WAH, weedy rice continued to produce more biomass at the highest N rate, but Drew did not respond substantially to added N. Weedy rice had more culm biomass (55% of total) than Drew (48%). Lower leaves constituted 16–19% of total shoot biomass, flag leaf 6%, and panicles comprised the rest for both plant types. In general, weedy rice accumulated more N, responded to higher N rates, accumulated more N in the panicles, and had a higher N use efficiency (for biomass production) than Drew rice. Weedy rice can accumulate 63% of fertilizer N, 2 WAH. We conclude that weedy rice responds to higher N rates, takes up more N, and has higher N use efficiency for biomass production than rice. Whenever a rice field is heavily infested with weedy rice, controlling weedy rice should be the priority. Otherwise, fertilizer N application (which is more expensive than weedy rice control) is not profitable.
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1. Introduction

Weedy or red rice (*Oryza sativa* L.) is a relative of cultivated rice (*O. sativa*), which infests rice production fields in the southern U.S. rice belt and various rice-producing regions worldwide. Where present, it quickly becomes the dominant weed because of its high competitive ability (Smith, 1988). Since the early 20th century, weedy rice has been reported as the worst weed in weedy rice-infested areas of the southern U.S. (Vincenheller, 1906) and still is today. Among 10 prevalent weeds in rice production in the southern U.S., including barnyardgrass (*Echinochloa crus-galli* L.), weedy rice caused the highest yield reduction in rice (about 80%) after season-long competition (Smith, 1988). One weedy rice plant per m^2 can reduce the yield of 'Newbonnet' rice, a tall cultivar, by 219 kg ha^{-1} (Smith, 1988). The competitive ability of one weedy rice plant was equivalent to three 'Mars' rice plants (Pantone and Baker, 1991). The competitive interaction is modified by the type of rice cultivar or biotype of weedy rice involved.

In flooded rice culture, nutrients and light quickly become the most limiting resources in the paddy micro-environment. By virtue of its size (tall, high tillering capacity, large leaf area), weedy rice avails of these resources more than the rice could under a competitive environment (Kwon et al., 1992). The optimum fertilizer N requirement, for currently grown rice cultivars in the United States, ranges from 134 to 202 kg N ha^{-1} (Norman et al., 2003). If weedy rice removes even just 50% of this, the yield of rice will be significantly reduced and economic returns from fertilizer application will be largely diminished. Fertilizer N uptake efficiency in rice can range from 10 to as high as 80% depending on how the N fertilizer is managed (Norman et al., 1992, 2003; Fageria and Barbosa Filho, 2001; Dobermann et al., 2002; Vlek and Byrnes, 1986; Wilson et al., 1998). This large range in N uptake efficiency of rice is because there are several N loss mechanisms that operate in a flooded soil that compete with the rice plant for available N. These mechanisms have received much attention from soil fertility scientists, but the competition from weeds or weedy rice on N uptake efficiency of rice has not been addressed (Norman et al., 2003). Thus, the degree to which weedy rice can compete with rice for fertilizer N is unknown. This information would be useful in farm management decisions pertaining to management of soil fertility in weedy rice-infested fields.

This research compared the relative efficiencies of rice and weedy rice in recovering applied fertilizer N under a competitive condition. Isotopic tracer ^{15}N was used to measure the fertilizer N uptake efficiencies of rice and weedy rice. N use efficiency of rice and weedy rice was compared in terms of shoot biomass production and the partitioning of biomass and accumulated N in shoot tissues.

2. Materials and methods

2.1. Site description and experimental design

Field experiments were conducted at the University of Arkansas Rice Research and Extension Center (RREC), Stuttgart, AR in 1999 and 2000 on a Dewitt silt loam (fine, smectitic, thermic, Typic Albaqualfs) soil. The experiment was arranged in a split–split plot design with four replicates. The main plot was N rate (0, 50, 100, 150 and 200 kg N ha^{-1}), the subplot was plant type (rice or weedy rice), and the sub-subplot was type of shoot tissue (lower leaf, leaf sheath, top leaf and panicles).

Rice 'Drew' and strawhull weedy rice were drill-seeded at 90 kg ha^{-1}, on May 7, 1999 and May 1, 2000, in alternate rows, 19 cm apart, 2.5 m long, with each plot consisting of eight rows. To prevent overcrowding the rice with weedy rice plants, one-half of the weedy rice seed was heat-killed and at the one- to two-leaf stage, weedy rice seedlings were thinned to a density equal to one-third of the rice density in each pair of row. Weedy rice cannot be grown at the same

density as rice without a severe impediment in rice growth (Kwon et al., 1991a) and incurring severe lodging of weedy rice plants at the reproductive stage. Drew is a long-grain cultivar developed in Arkansas, released in 1996, and was chosen because it was high-yielding and widely planted in the southern U.S. rice belt at the time the experiments were conducted, until today. It has mid-season maturity range (about 125 days after emergence) and is 110 cm tall (Moldenhauer et al., 1998). Strawhull weedy rice is the most prevalent type of weedy rice in the southern U.S. The type used in this experiment represents the majority of the strawhull weedy rice types, which matures early (about 100 days after emergence) and is taller (about 145 cm) than rice. Prior to planting, 224 kg ha^{-1} of commercial fertilizer (0–40–60) was applied to the entire block where the experiment was located. The N fertilizer treatments were applied at 26–27 days after emergence (DAE) as ^{15}N-labeled pelletized urea (2.217 at% ^{15}N, 2.4 mm × 3.0 mm), evenly distributed by hand, into microplots bounded by galvanized steel frames (76.2 cm × 76.2 cm × 30.5 cm), which were driven into the ground 15 cm deep (Fig. 1). No applied N could move out of this microplot. Each square had two rows each of rice and weedy rice. After application of ^{15}N-labeled urea, the metal squares were covered with plastic sheets and commercial urea (46–0–0) was spread over the entire experiment at 100 kg N ha^{-1}. Each N rate was applied to two metal squares per replication; one was harvested at panicle initiation (PI) and the other was harvested at 2 weeks after heading (WAH). The entire experiment was flooded immediately after N application. The microplots were manually filled with water to the same level (5–10 cm depth)
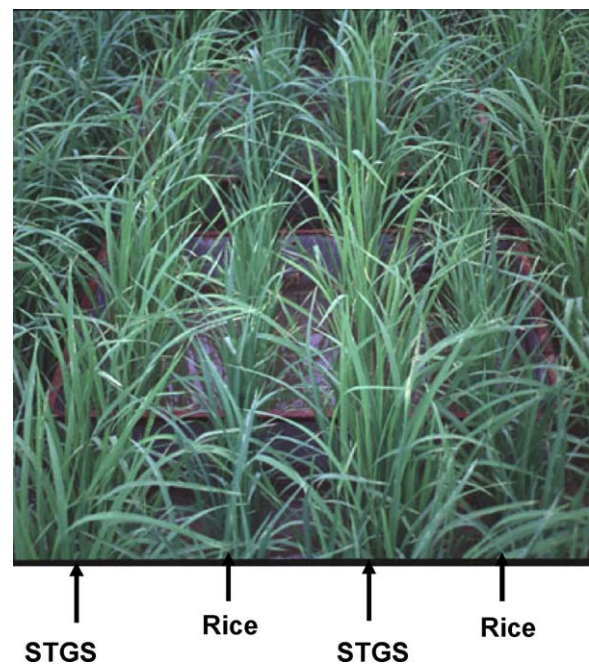

Fig. 1. Alternate rows of weedy rice (Stuttgart strawhull red rice) and rice, with the metal frame enclosing two rows of each. Rice Research and Extension Center, Stuttgart, Arkansas, USA.

as the rest of the field. Water level in the microplots was checked twice each week, and replenished as needed.

For weed control, propanil [*N*-(3,4-dichlorophenyl)propanamide] at 3.4 kg ai ha^{-1} mixed with thiobencarb [*S*-[(4-chlorophenyl)methyl]diethylcarbamothioate] was applied at 2.24 kg ai ha^{-1} 5 DAE. This was followed by another application of propanil at 4.48 kg ai ha^{-1} mixed with quinclorac (3,7-dichloro-8-quinolinecarboxylic acid) at 0.56 kg ai ha^{-1} 20 DAE.

2.2. Data collection

Plant samples were collected by cutting shoot tissues, from the two rows of rice and two rows of weedy rice, at the soil surface. Plant samples were placed in plastic bags, immediately placed in a cooler with ice, and transported to the laboratory where the aboveground biomass was separated into bottom leaves, leaf sheath (culm) and upper leaves for the first sampling at PI. The upper leaves included all unfolded leaves and the youngest, fully expanded leaf with visible collar, all of which were cut at the collar region of the fully expanded leaf. For the second sampling, 2 WAH, the harvested samples were separated likewise, with the panicle as an additional shoot biomass component. At this development stage, the top leaf was composed only of the flag leaf. Each part was placed in a paper bag and oven-dried at 60 °C to a constant weight, the dry weights were recorded, the tissues were ground to pass a 425-μm sieve, and a subsample was taken for N analysis.

Total N of plant material was determined on a 0.2-g subsample by the permanganate-reduced Fe modification of the semimicro-Kjeldahl procedure (Bremmer and Mulvaney, 1982). The distillation apparatus was cleaned between each sample by the duplicate aliquot procedure to prevent ^{15}N cross-contamination (Mulvaney, 1986). Distillates were then evaporated to dryness for ^{15}N analysis and at% ^{15}N was determined at the University of Illinois on Nucleide 3-60-RMS double collector mass spectrometer (Measurement and Analysis Systems, Belefonte, PA) according to procedures described by Mulvaney et al. (1990).

Data were analyzed separately by growth stage, using general linear models (GLM) procedure in SAS software (SAS, 2004), with year as a random variable.

3. Results

3.1. Dry matter accumulation and partitioning

At PI, there was no three-way interaction between N rate, type of plant, and type of shoot tissue on shoot biomass accumulation and partitioning. The main effects of each factor, however, were significant. The interaction between N rate and plant type on the accumulation of total shoot biomass was significant ($p = 0.011$) (Fig. 2). Drew and weedy rice produced 207 and 239 g m^{-2} shoot biomass, respectively
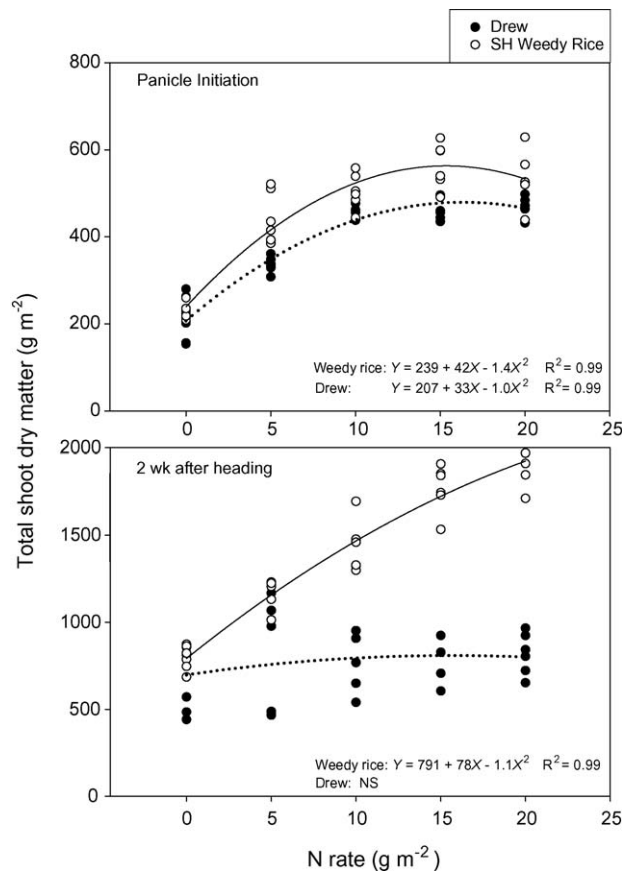

Fig. 2. The effect of N rate on total shoot biomass production of 'Drew' rice and strawhull weedy rice at panicle initiation and 2 weeks after heading (WAH), grown under competitive condition, at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

when no N fertilizer was applied, but these were statistically similar. Both plant types showed a typical quadratic response to N fertilizer (Drew: $Y = 207 + 33X - 1.0X^2$; weedy rice: $Y = 239 + 42X - 1.4X^2$). This means that the response to added N diminished with N rate and eventually became negative beyond 16 and 18 g m^{-2} N, respectively, for weedy rice and Drew. Despite showing the same type of relationship between biomass production and N level, weedy rice produced more biomass than Drew whenever N fertilizer was applied. Where the response to added N was positive, weedy rice showed a higher rate of response (42 g biomass g^{-1} N) than Drew (33 g biomass g^{-1} N). Drew and weedy rice continued to produce more biomass, although at declining increments, in response to fertilizer N application up to the 16 and 15 g N m^{-2} rate, respectively.

At 2 WAH, a significant interaction was also observed between N rate and plant type on total shoot biomass accumulation (Fig. 2). Drew and weedy rice had equivalent total shoot biomass when no N fertilizer was applied, but the addition of N elicited a higher response from weedy rice than that of Drew. Weedy rice showed diminishing response to added N as was observed at PI ($Y = 791 + 78X - 1.1X^2$), but at heading, shoot biomass continued to increase up to the highest N rate instead of reaching a maximum. On the other

hand, Drew showed minimal response to additional N in terms of shoot biomass production at this stage. Drew produced $686\,\mathrm{g\,m^{-2}}$ shoot biomass without fertilizer N. This increased to an average of $862\,\mathrm{g\,m^{-2}}$ biomass with N fertilizer, but independent of rate. The difference in biomass accumulation in response to N rate between Drew and weedy rice was much larger at 2 WAH than at PI.

Shoot biomass partitioning at PI, between Drew and weedy rice was similar. Logically, the proportion of each plant part relative to the total shoot biomass was different ($p < 0.0001$). The proportion of lower leaf biomass relative to total shoot biomass remained constant at about 30% regardless of N dose (data not shown). Leaf sheath comprised 48% of shoot biomass, averaged over the two plant types. Shoot biomass partitioned differently between N rate, plant type, and type of tissue ($p = 0.008$) at 2 WAH. There was generally no difference between Drew and weedy rice in terms of shoot biomass partitioning to lower leaves (Fig. 3). The flag leaf biomass of Drew was not affected by N rate, but that of weedy rice showed a quadratic response to added N ($Y = 45.7 + 5.8X - 0.1X^2$) as was observed with lower leaf ($Y = 148.8 + 10.9X - 0.2X^2$), leaf sheath ($Y = 492.8 + 43.1X - 0.9X^2$), and total biomass accumulation. In general, the proportion of shoot biomass in lower leaves (16–19% of total) and flag leaf (6% of total) was not

affected by N rate. For weedy rice, the leaf sheath comprised 54–60% of total shoot biomass, the proportion of which declined relative to increasing N rates. Leaf sheath comprised the bulk of shoot biomass in both plant types, but weedy rice had a higher proportion of its biomass from stems (55%) compared with Drew (48%), on an average. Partitioning of biomass to panicles in weedy rice increased with increasing N rates ($Y = 132.4 + 17.3X$), from 16 to 27% of total and is contrary to what was observed for Drew panicles. With Drew, biomass of panicles declined with N rate ($Y = 350.8\,\mathrm{e}^{-0.04X}$).

3.2. Total N uptake and partitioning

At PI, Drew and weedy rice showed different patterns of total N accumulation with respect to N rate (Fig. 4). At this stage, both plant types showed a linear pattern of fertilizer N accumulation; however, weedy rice showed a higher rate of N accumulation (0.61 g N in shoot tissue $\mathrm{g^{-1}}$ fertilizer applied) than Drew (0.33 g N in shoot tissue $\mathrm{g^{-1}}$ fertilizer applied). Total N partitioned differently between shoot tissues in both plant types (data not shown). The proportion of total N accumulated in lower leaves of Drew and weedy rice was similar and was not affected by N rate (39–43% of total N) (data not shown). The allocation of total N to the
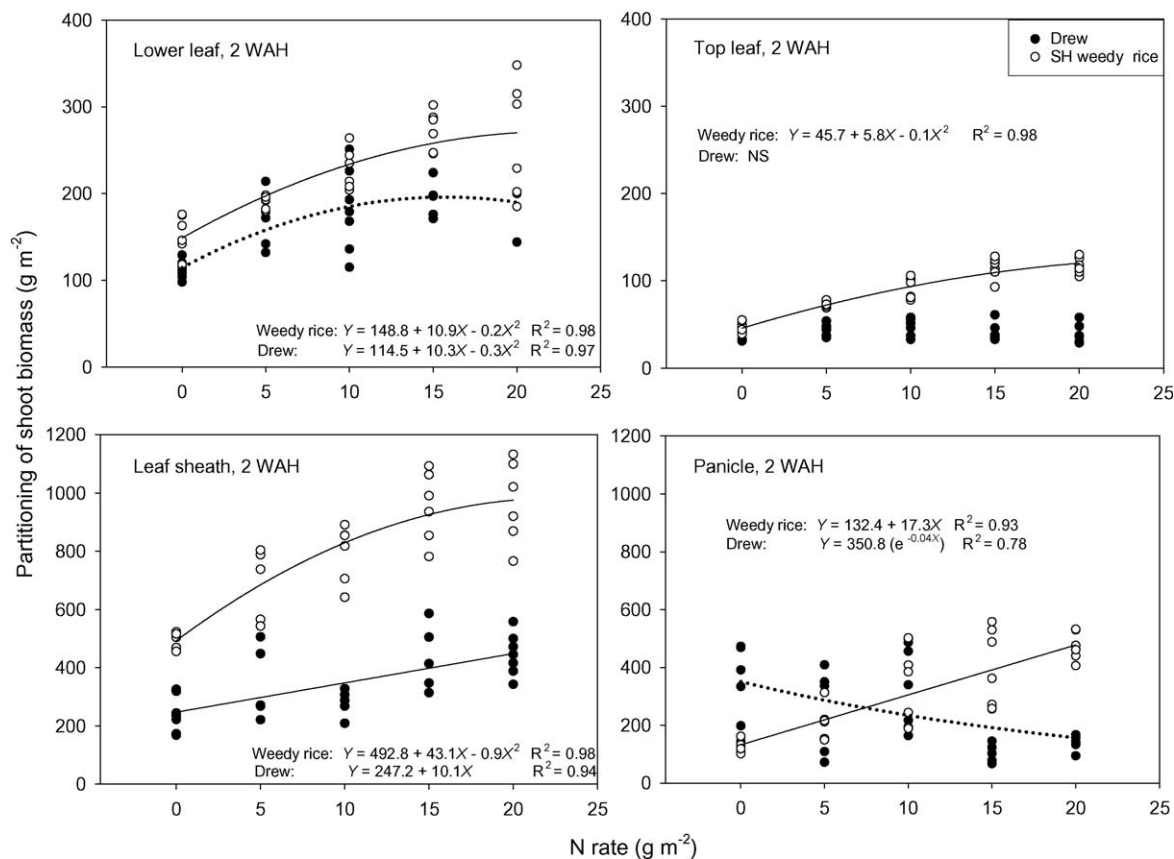

Fig. 3. Proportion of shoot biomass partitioned into various shoot tissues of Drew rice and strawhull weedy rice, grown under competitive condition, 2 weeks after heading (WAH) in response to fertilizer N applied 26–27 days after emergence, immediately before flooding, at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.
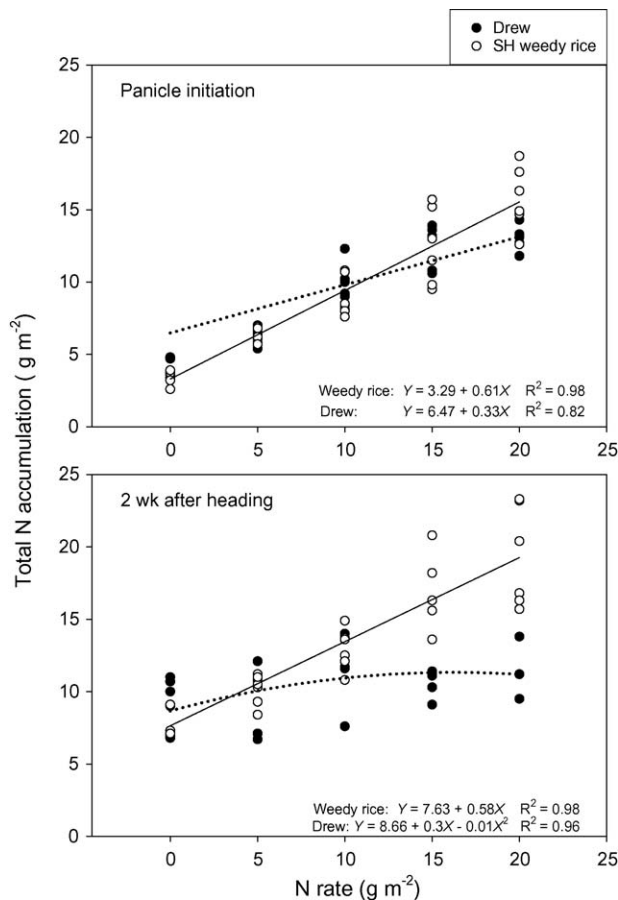
Fig. 4. Total N accumulated in all shoot tissues of 'Drew' rice and strawhull weedy rice at panicle initiation and 2 weeks after heading (WAH), grown under competitive condition, as affected by rate of fertilizer N applied 26–27 days after emergence, immediately before flooding, at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

other plant parts of weedy rice was also not affected by N rate; this ranged from 28 to 30% in the leaf sheath and 27 to 33% in the top leaves. On the other hand, Drew showed a decline in proportion of total N in the leaf sheath as N rate increased, with 36% at $0 \, g \, m^{-2}$ applied N to 23% at $20 \, g \, m^{-2}$ applied N (data not shown). This was accompanied by a corresponding increase in the proportion of total N accumulated in the top leaves of Drew with increased N fertilizer rate. Averaged over N rates, the amount of total N taken up was highest in the lower leaves (40% of applied) although shoot biomass was principally comprised of leaf sheath. Equivalent amounts of total N accumulated in the leaf sheath (29% of applied) and top leaves (30% of applied) although the biomass of top leaves was only about one-half of the leaf sheath biomass (data not shown).

At 2 WAH, there was a significant interaction between plant type and N rate on total N accumulated in all shoot tissues (Fig. 4). Total N uptake pertains to accumulation of native soil N + fertilizer N in the plant. The overall total N uptake by weedy rice followed a linear pattern ($Y = 7.63 + 0.58X$) as opposed to its quadratic response in shoot biomass production relative to fertilizer N addition. Total N accumulation by

weedy rice continued to increase at the same rate within the range of fertilizer level tested. With $20 \, g \, m^{-2}$ applied N, weedy rice accumulated $19.3 \, g \, m^{-2}$ total N in shoot tissue. Drew, on the other hand, showed a declining rate of N uptake with increasing levels of added N ($Y = 8.66 + 0.3X - 0.01X^2$). The maximum N accumulation for Drew occurred at 15.4 g applied N m^{-2} with $11.32 \, g \, m^{-2}$ total N accumulated. It was apparent that Drew did not obtain as much N as weedy rice at the higher N rates. Overall, the relationship of total N uptake by Drew and fertilizer N rate was weak. This was unlike what was observed at PI. Interestingly, there was no difference in total N uptake between Drew and weedy rice at the lower N rates but weedy rice accumulated more N than Drew at N fertilizer rates beyond $8 \, g \, m^{-2}$. A three-way interaction of N rate, plant type, and type of tissue was observed ($p = 0.001$) and the main effects of these factors on total N accumulation were significant. Partitioning of total N in various shoot tissues is as follows (data not shown). Total N in the lower leaves and leaf sheath generally increased with N rate in both plant, but total N accumulated by weedy rice in these tissues was generally greater than that of Drew. Total N in the flag leaves of Drew was not affected by N rate, but generally increased with N rate in weedy rice. Total N accumulated in the panicles increased with N rate in weedy rice, but the reverse was observed in Drew.

The proportion of total N from all above-ground parts that accumulated into various tissues, averaged over N rates, in Drew was as follows: lower leaf > panicle > leaf sheath > flag leaf and in weedy rice: lower leaf > leaf sheath > panicle > flag leaf. The proportion of total N accumulated in lower leaves of Drew most closely followed a cubic function, where there was a lag in N accumulation at the lowest N rate, followed by a linear response to additional fertilizer N up to $14 \, g \, m^{-2}$. The maximum proportion of total N accumulated in the lower leaves was 44%, which occurred at $16.5 \, g \, m^{-2}$ N rate. Beyond this level, the rate of allocation of total N in lower leaves of Drew started to decline (Fig. 5). Weedy rice showed an inverse linear relationship between the proportion of total N accumulated in lower leaves and the rate of fertilizer N applied. The highest proportion of N accumulation in lower leaves of weedy rice occurred when no fertilizer N was applied (35% of total N). As total N accumulated by the above-ground tissues of weedy rice plant increased with N rate, the proportion of total N in lower leaves declined by $0.32\% \, g^{-1}$ of added N. The proportion of total N in the leaf sheath of Drew increased with N rate, but the proportion of total N in panicles declined greatly (from 45 to 18% of total) as fertilizer N level increased from 0 to $20 \, g \, m^{-2}$. Weedy rice showed similar partitioning (26–30%) of total N into leaf sheath regardless of N rate, but it accumulated an increasing proportion of total N (18–28%) in its panicles as N level increased. While the proportion of total N in lower leaves of Drew increased, up to a point, the proportion of total N in its panicles decreased. The decline in total N allocation to panicles of Drew most closely followed an exponential decay pattern where the rate of decline was initially faster at
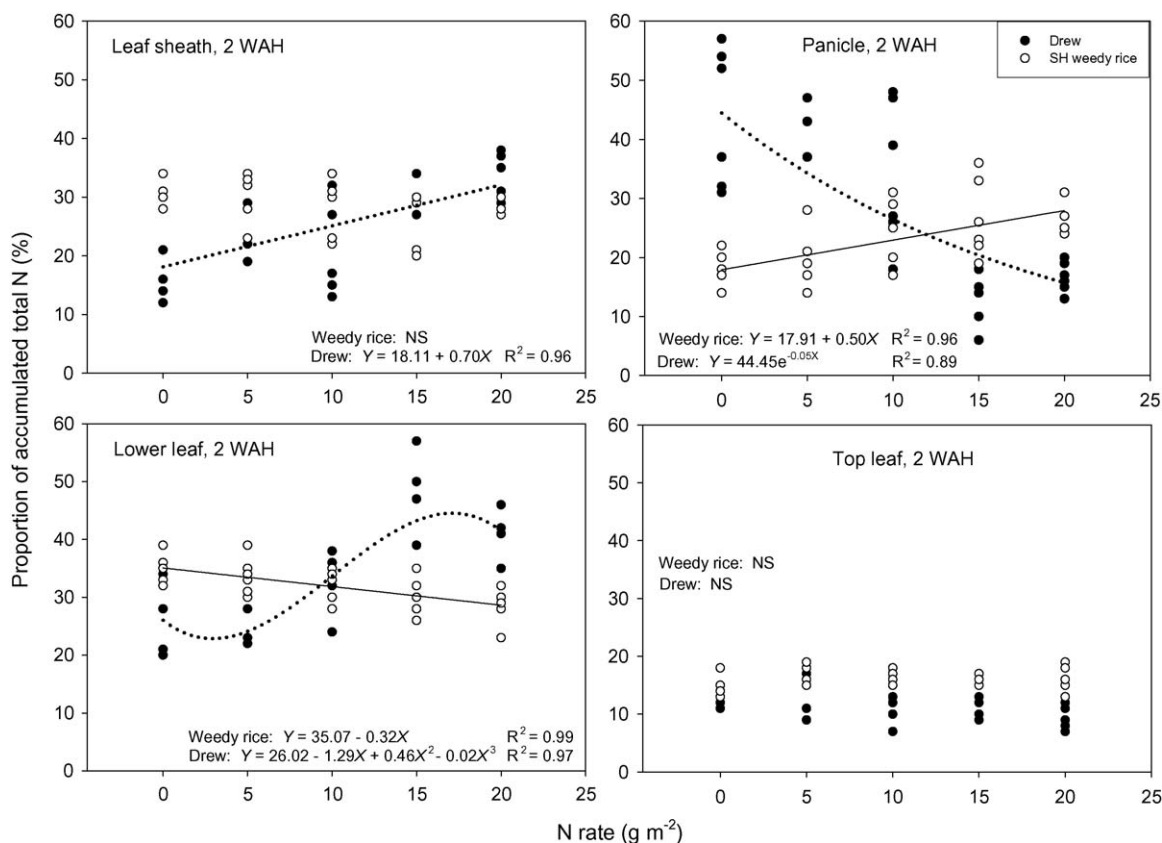
Fig. 5. Proportion of total N accumulated partitioned into various shoot tissues of Drew rice and strawhull weedy rice, grown under competitive condition, 2 weeks after heading (WAH) in response to fertilizer N applied 26–27 days after emergence, immediately before flooding, at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

lower N rates and gradually slowed down as more fertilizer N was added. Drew started with 44% of total N accumulated in panicles when no N was applied and ended up with 16% at 20 g m^{-2} N rate, which was lower than that in the panicles of weedy rice at this level of fertilizer N.

3.3. Fertilizer N uptake

The percentage of fertilizer N taken up by weedy rice increased linearly with N rate (56–75%) at PI (Fig. 6). Fertilizer N accumulation in weedy rice did not reach a peak within the range of fertilizer level used in this experiment. Drew, on the other hand, showed only a slight increase in the percentage of fertilizer N accumulated up to the 11.1 g N m^{-2} rate (62–67%) and then fertilizer N accumulation decreased significantly thereafter. Fertilizer N partitioned similarly into different tissues of both plant types. The proportion of fertilizer N accumulated in lower leaves of Drew and weedy rice was similar and was not affected by N rate (42–47% of total accumulated fertilizer N) (data not shown). The allocation of fertilizer N to the other plant parts of weedy rice was also not affected by N rate; this ranged from 26 to 27% in the leaf sheath and 26 to 31% in the top leaves. Drew had 23–28% of accumulated fertilizer N in the leaf sheath and 27–34% in the top leaves, but these values were independent of applied N rate (data not

shown). Averaged over N rates and plant type, the proportion of fertilizer N accumulated was highest in the lower leaves (41% of fertilizer N) although shoot biomass was principally comprised of leaf sheath. The proportion of fertilizer N in leaf sheath was 28% and that in top leaves was 31% of total accumulated ^{15}N (data not shown).

Fertilizer N accumulation in Drew, 2 WAH, declined linearly with N rate ($Y = 59.3 - 1.2X$) (Fig. 6). Drew accumulated 53% of applied N at 5 g m^{-2} N rate, but only 35% of applied N at the 20 g m^{-2} N rate. On the other hand, weedy rice accumulated a similar proportion (59%) of applied N at the at 5 g m^{-2} N rate, but this was not affected by fertilizer N level. Weedy rice acquired 63% of applied N, averaged over N rates.

Fertilizer N partitioned differently at 2 WAH, with respect to plant type, tissue, and N rate. In general, the proportion of applied fertilizer N in the lower leaves of Drew was lesser than that in weedy rice, regardless of N rate. Partitioning of fertilizer N into the lower leaves of weedy rice showed a slight, but significant increase from 18.3% at 5.0 g m^{-2} N to 22.4% at 20 g m^{-2} N rate ($Y = 16.93 + 0.27X$) (Fig. 7). The proportion of fertilizer N accumulated in the leaf sheath (17%), flagleaf (10%), and panicle (14%) of weedy rice was not affected by N rate. The proportion of fertilizer N in the leaf sheath of Drew (12%) was also not affected by N rate. This was lower than what was found in the leaf sheath of weedy
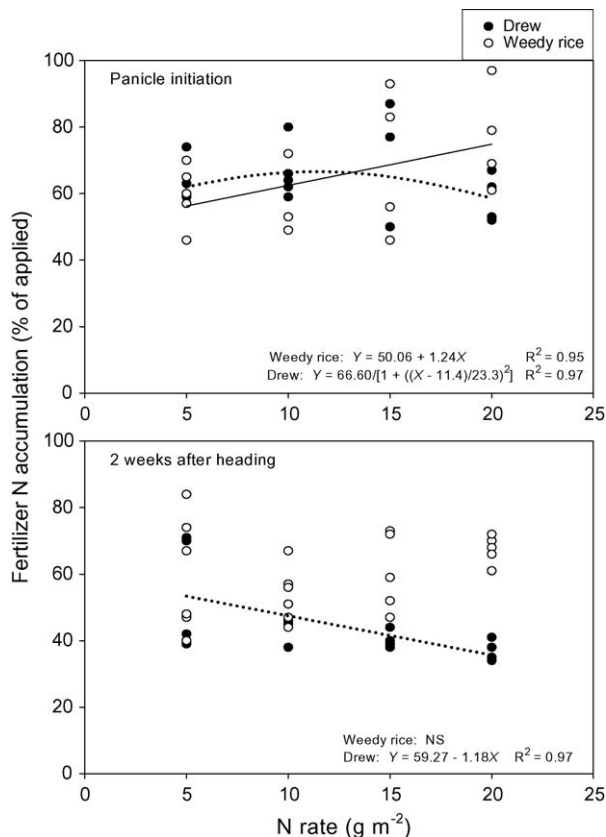
Fig. 6. Relative efficiencies of Drew rice and strawhull weedy rice in recovering ^{15}N fertilizer, applied 26–27 days after emergence, at panicle initiation and 2 weeks after heading (WAH) at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

rice. Partitioning of fertilizer N to the flag leaves of Drew decreased slightly, but significantly, with increased N rate. Overall, weedy rice also had a higher proportion of fertilizer accumulated in the flag leaves than Drew. Fertilizer N accumulation in the panicles of Drew declined exponentially with increased N rate. Initially, Drew had 17.2% of fertilizer in its panicles at 5 g m^{-2} N, which was similar to that of weedy rice. However, while the proportion of fertilizer N in panicles of weedy rice remained about the same, that of Drew declined to 4.6% at 20 g m^{-2} N rate. The difference in the proportion of fertilizer N in the panicles of Drew and weedy rice became larger as N rate increased.

3.4. N use efficiency for biomass production

The rate of shoot biomass production for every unit of total N accumulated (N use efficiency), in Drew and weedy rice, was presented as a function of N rate. At PI, Drew and weedy rice produced equivalent amounts of shoot biomass g^{-1} of total N accumulated, when no fertilizer N was added (69 and 72 g g^{-1}, respectively) (Fig. 8). N use efficiency for Drew ($Y = 65.02 - 1.6X$) and weedy rice ($Y = 71.56 - 1.6X$) declined linearly with increasing N rate. N use efficiency in both plant type declined by 1.6 g g^{-1} of additional N accumulated. However, weedy rice produced significantly

more shoot biomass per unit of total N accumulated than Drew, averaged over N rate. The average efficiency of weedy rice in producing biomass per unit of N accumulated was 56 g g^{-1} whereas that of Drew was 47 g g^{-1}.

At 2 WAH, there was also no significant interaction effect between N rate and plant type on N use efficiency as was observed at PI. However, unlike at PI, N use efficiency for Drew linearly declined with N rate ($Y = 79.7 - 0.52X$) while that of weedy rice showed a peak, which was most closely described by a Lorentzian function [$Y = 114/[1 + ((X - 7.6)/27.0)^2]$]. The maximum N use efficiency for weedy rice was observed at 7.42 g N m^{-2}. At this N fertility level, weedy rice produced about 113.91 g shoot biomass g^{-1} total N accumulated whereas Drew produced only 75.80 g biomass g^{-1} N accumulated. Regardless of N rate, the N use efficiency of weedy rice was higher than that of Drew.

4. Discussion

The 'law of diminishing returns' was apparent in the response of rice and weedy rice to fertilizer N in terms of biomass production. It is important to note that this was observed in a situation where Drew rice and weedy rice were competing for N. The distribution of weedy rice among cultivated rice in this experiment is not typical of natural occurrence in rice fields, but the ratio of rice to weedy rice was kept at a level commonly encountered in heavily infested fields. Planting the weedy rice in rows facilitates accurate sampling of plants without reducing the degree of interference between plant types. The close row spacing (19 cm) still allowed for maximum above- and below-ground competition. At the early tillering stage, which was around 4 weeks after emergence, the canopy of Drew and weedy rice had already started to overlap (Fig. 1). Weedy rice, being taller and bigger, exerted severe competition for light. The primary reason for keeping the density of weedy rice at one-third the density of Drew, even in this planting arrangement, is to keep the weed from eliminating the crop. This row spacing also allows for below-ground interference because roots of rice or weedy rice are able to occupy the full width of 26 cm-diameter pots at PI (unpublished data). The biomass accumulation of Drew and weedy rice in response to added N became negative beyond 18- and 16-g N m^{-2}, respectively, most likely because other factors such as light or other nutrients (i.e., P and K) had become limiting. This type of response to production input is typical (Tisdale et al., 1993); however, the N rate that would elicit declining response from Drew in a rice monoculture situation could be higher because of reduced level of competition. When the plant continues to absorb nutrients without added response in terms of plant growth or yield, luxury consumption is occurring. Luxury consumption was observed in both plant types at higher N rate at PI, meaning, a point was reached when plants had more than sufficient available N. This was supported by the declining N use efficiency with increasing N rate.
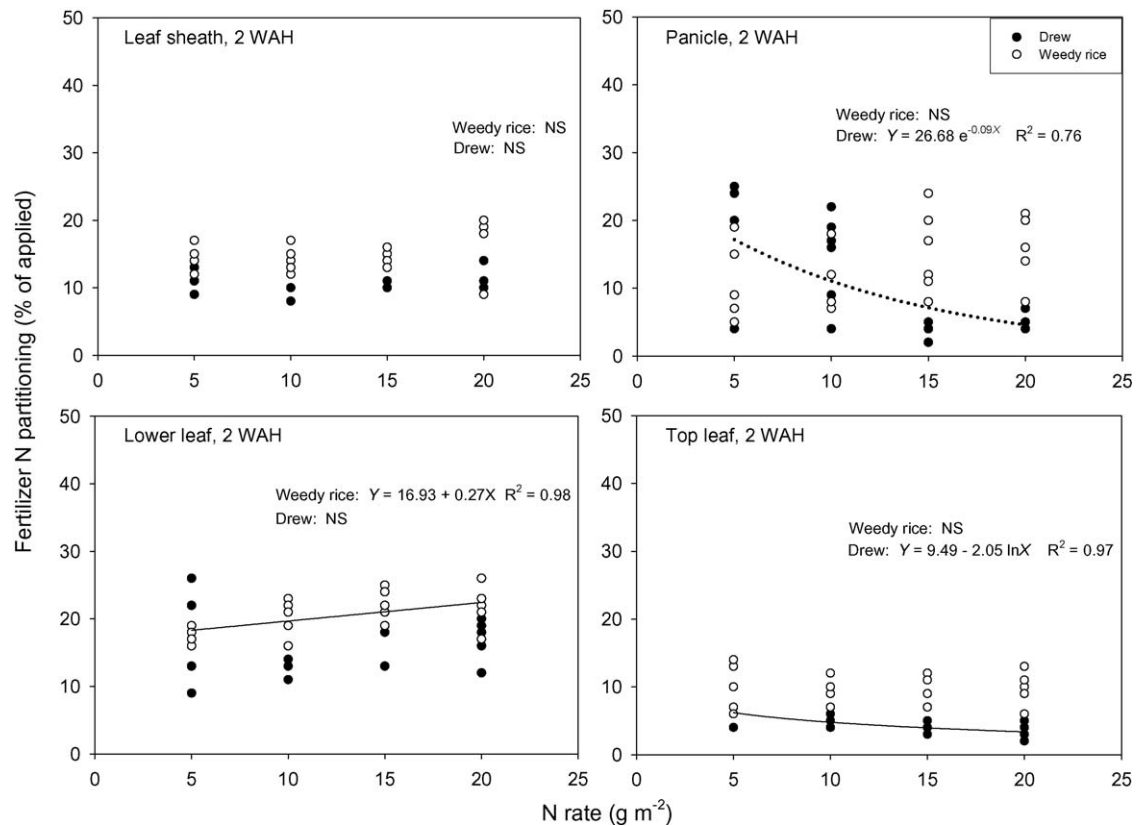
Fig. 7. Partitioning of fertilizer N accumulated into various shoot tissues of Drew rice and strawhull weedy rice, grown under a competitive condition, 2 weeks after heading (WAH) in response to fertilizer N applied 26–27 days after emergence, immediately before flooding, at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

Weedy rice apparently did not reach a plateau in biomass production even at the highest rate of N applied (20 g m^{-2}) 2 WAH, indicating that its demand for N increased with age and had continued into the later reproductive stage. It is important to note though, that the quadratic response in biomass production at heading was indicative of declining response to added N at higher N rates. The peak and subsequent decline in N use efficiency at 2 WAH corroborated this. Weedy rice became a bigger plant and more aggressive competitor than rice and this caused the atypical response of Drew to fertilizer N. Drew showed minimal response to added N when vegetative growth was supposed to be maximized and grains were filling. The reduced N use efficiency in Drew was coupled with lesser total N accumulation compared with weedy rice. In Arkansas production fields, the optimum fertilizer N rate for Drew is 118 kg ha^{-1} for a single, preflood application (Wilson et al., 2001), as was done here. The low response to fertilizer N in Drew was due to the substantial removal of available N by weedy rice (63% of applied) and the lower capacity of Drew to produce shoot biomass for every unit of N accumulated. Overall, this resulted in a much larger difference in biomass accumulation between weedy rice and Drew at 2 WAH compared with that observed at PI. Previous studies have shown that weedy rice is a much better competitor than rice, causing 34 and 58% reduction in shoot dry weights of Newbonnet and Lemont rice, respectively, at

weedy rice interference duration of up to 120 DAE (Kwon et al., 1991b). Previous studies on competition between rice and weedy rice, such as those cited in this paper, were done either as field experiments with varying weedy rice densities or as replacement series pot experiments with various rice: weedy rice proportions. Whereas, in our experiment the proportion of rice and weedy rice was held constant while the N level varied. The low biomass accumulation response of Drew to fertilizer N at 2 WAH, coupled with the decline in N uptake by Drew at the high N rates, indicate that Drew was: (i) being out competed for N at the high N rates by the weedy rice and/or (ii) out competed by weedy rice in biomass production whenever N was applied. The atypical N accumulation and biomass production by Drew at the high N rates was probably due to the interaction with the weedy rice.

The fact that weedy rice had a higher proportion of shoot biomass from culm tissues at the later growth stage was because weedy rice is a taller plant than Drew, but with the same total number of leaves, 15–16, per culm (Stiers, 2002). The weak relationship between culm biomass and added N for Drew indicates that when growing in competition with weedy rice, fertilizer N addition did not significantly increase tiller production and, even resulted in reduced panicle production at higher N rates. In this experiment, however, culm and panicle numbers were not recorded. Although the number of panicles was not recorded, it was observed that weedy rice produced
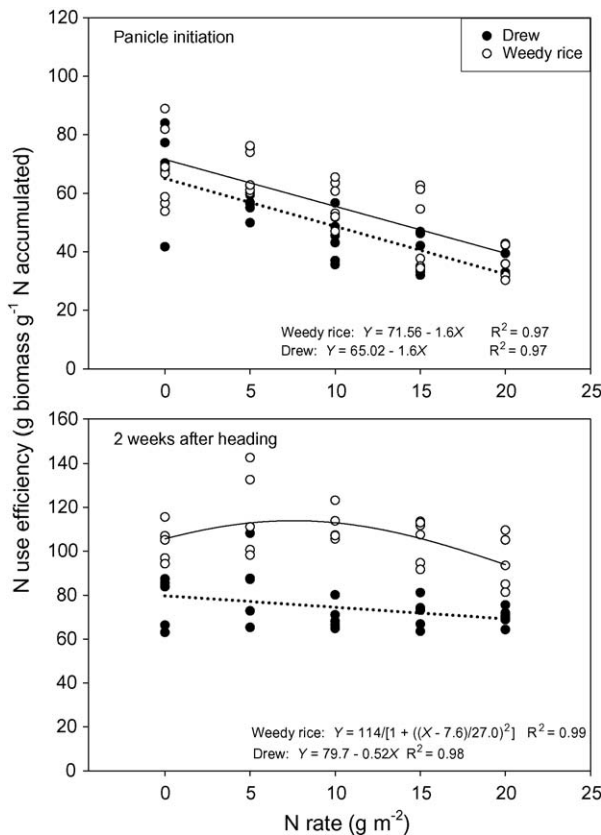
Fig. 8. N use efficiency of Drew rice and strawhull weedy rice in terms of biomass production, under competitive condition, as affected by fertilizer N rate at panicle initiation and 2 weeks after heading (WAH), at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.

bigger and more panicles than Drew as more N was added. The panicle biomass supported this.

As was observed with shoot biomass, the difference in total N uptake (native + fertilizer N) between Drew and weedy rice became larger at 2 WAH than at PI. Simply, this means that the weedy rice was able to accumulate a larger proportion of available fertilizer and soil N than Drew by 2 WAH, which was corroborated by higher N accumulation in weedy rice at this stage. The limited increase in total N accumulation in Drew shoots at heading ($0.3 \, g \, g^{-1}$ of applied N), and the subsequent decline in total N accumulation rate, was most probably a reflection of inadequate N for Drew, as the consumption of N by weedy rice continued to rise. The reduced panicle biomass of Drew at higher N rate implies that it is useless to apply N fertilizer to a field that is heavily infested with weedy rice. It makes the weed grow bigger thereby choking the crop. It was tempting to say that weedy rice translocated more of its accumulated N to the panicle than Drew did, but this was confounded by the fact that Drew produced less panicle biomass than weedy rice. However, the fact that the proportion of total N in the panicles of Drew declined at the point where the proportion of total N in the lower leaves increased, indicates that Drew was not able to translocate this accumulated N effectively to the developing panicles. In contrast, the proportion of total N in lower leaves

of weedy rice declined while total N accumulation increased with increased N rate. This indicates the ability of weedy rice to move N to the upper shoot tissues where it was more needed. Under optimum production conditions ($134 \, kg \, N \, ha^{-1}$), without weedy rice competition, 60% of shoot N in rice was found in leaves just prior to heading and there was no difference in N partitioning regardless of cultivar stature (Norman et al., 1992). Nitrogen accumulation in the panicles increased immediately after heading, at the expense of other plant parts (Norman et al., 1992). In our experiment, when rice was grown in competition with weedy rice, the maximum N uptake was observed at $154 \, kg \, N \, ha^{-1}$, which was about the recommended N rate for Drew. Beyond this point, N uptake tapered off not because Drew already had enough N, but probably because it had already extracted the most that was available from the soil under these circumstances. Incidentally, $150 \, kg \, N \, ha^{-1}$ is the recommended N rate for most of the rice cultivars grown in the southern United States (Wilson et al., 2001). At lower N rates, the highest proportion of total N was found in the panicles just as Norman et al. (1992) observed with other rice cultivars, but at higher N rates, the proportion of N in panicles of Drew rice declined and remained mostly in the lower leaves. This reflected the fact that the proportion of panicle biomass in Drew declined with increasing N rate. In this situation, less N was available to Drew and it was also shaded by the weedy rice, which had grown taller and more robust at high N rates. This led to reduced productive tillers and reduced panicle development in Drew. In weedy rice, allocation of total N to the panicles and the proportion captured in the culm remained more or less the same, as the proportion of total N in the lower leaves decreased. This indicates that weedy rice was better able to translocate N to the panicles.

The maximum amount of fertilizer N recovered by Drew at PI (67% at $11.1 \, g \, m^{-2}$ N rate) was comparable to the maximum figures reported by Norman et al. (1992). However, the decline in accumulation of fertilizer beyond this point reflected the competition exerted by weedy rice, which became apparent at the highest N rate. When averaged across N rates both Drew and weedy rice accumulated comparable proportions of applied N (62 and 66%, respectively). This means that up to PI, the competition for fertilizer N was not yet as intense as what would be observed at 2 WAH. At the early growth stage, weedy rice continued to accumulate more N as fertilizer level increased therefore, it had eventually accumulated a much larger amount of fertilizer N at 2 WAH than Drew. Also, weedy rice was more efficient than Drew in producing shoot biomass. There are two main reasons why weedy rice is able to take up more N than Drew or probably any cultivated rice (Diarra et al., 1985; Estorninos et al., 2002; Stiers, 2002). First, weedy rice is a big plant. Weedy rice continues to produce tillers throughout the growing season whereas rice ceases tiller production at the onset of reproductive stage (Moldenhauer and Slaton, 2001; Stiers, 2002). During the vegetative stage, the developing tillers act

as sink for nutrients thereby, maintaining a diffusion gradient of [N] from the roots to the young shoot tissues, encouraging more N accumulation. This results in more foliage, which could act as a reservoir of accumulated N (Norman et al., 1992). During the reproductive stage, more tillers mean more panicles and so the sink is shifted to the developing panicles. The use of a labeled N source showed a significant difference in the partitioning of fertilizer N to the developing panicles of weedy rice and Drew. The ability of a plant to move nutrients from source to sink tissues is one factor for increased productivity. Unlike weedy rice, the partitioning of N to developing panicles of Drew decreased with N rate. This was coupled by a negative relationship between fertilizer N accumulation in the flag leaves of Drew with N rate. One reason for this could be that weedy rice became a more aggressive competitor at the later growth stage, causing shading and nutrient stress to rice. This resulted in reduced panicle biomass of rice. Although the number of panicles was not determined in this study, it has been shown that the number of panicles plant^{-1} and florets panicle^{-1} are the primary yield components that are affected by competition (Pantone et al., 1992). The second reason for higher N uptake and recovery of applied N by weedy rice is its large root system. At 80 days after emergence, strawhull red rice produced 1.7–1.8 times more root mass than Bengal or Wells rice when grown individually in large pots at optimum soil fertility level (Stiers, 2002).

How much weedy rice had directly reduced the N uptake capacity of Drew could not be completely answered in this study because a monoculture planting of Drew was not done at all N fertilizer rates. However, there has been strong evidence from previous research that weedy rice is a much stronger competitor for resources than rice cultivars like Drew (Estorninos et al., 2002; Pantone and Baker, 1991) and the atypical N accumulation and biomass response of Drew to increasing N rate strongly suggests that the weedy rice greatly influenced Drew growth. This experiment confirmed that the bulk of applied fertilizer N went to weedy rice, its competitiveness increased with N rate, and its ability to produce biomass for every unit of absorbed N was higher than that of cultivated rice.

Acknowledgment

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